

ADAPTATION TO CHEMICAL STIMULATION OF THE TARSAL RECEPTORS OF THE BLOWFLY¹

V. G. DETHIER

Dept. of Biology, Johns Hopkins University, Baltimore 18, Maryland

In the course of several decades of studies of chemoreception in insects the existence of some demonstrable form of adaptation was speculated upon by many workers. Some actually designed specific experiments to develop the idea. These experiments usually took the form of a comparison of a taste threshold measured by means of a descending series of concentrations with a threshold obtained by ascending presentation. Among the investigators who made the comparison, Marshall (1935) and Eger (1937) could demonstrate no difference; Verlaine (1927), Weis (1930) and Kunze (1933) believed that such differences existed, but their data in support of the belief are statistically poor; von Frisch (1934) could detect no change in threshold but did observe modifications of behavior which suggested that adaptation did occur; Minnich (1929) observed clear-cut differences in threshold. Both during and since that period extensive use was made of a convenient reflex of flies and butterflies, the proboscis response; but the data which the method yielded in the hands of the pioneer workers were contradictory and of questionable significance. Now, as a consequence of recent advances in the field, fuller advantage may be taken of this easily observed and decisive response to investigate profitably the phenomenon of adaptation and to reconcile the divergent older results.

When receptors located on the tarsi are stimulated by solutions of certain sugars, among them being sucrose, glucose and fructose, the insect responds by extending its proboscis and, when permitted, by drinking. Upon cessation of stimulation or initiation of stimulation by a wide variety of non-saccharide materials (*e.g.*, electrolytes and many organic compounds) the proboscis, if extended, is retracted. If, prior to stimulation by unacceptable compounds, the proboscis is already in the retracted position, there is no discernible response involving the mouthparts. In order to study the stimulating effect of unacceptable compounds it has been the custom to mix different amounts of the material in question with sugar solutions which are then presented to the insects. In this manner one is able to ascertain the minimum concentration of an unacceptable compound which will prevent a response to sugar. Thus, the two basic techniques employed in all experiments on contact chemoreception involve the determination of acceptance thresholds and of rejection thresholds.

Any of three standard operational procedures may be followed in obtaining threshold data: (1) each insect of a sample population of two hundred or more is stimulated by each concentration in turn presented in ascending order until a

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response is obtained; (2) each fly is stimulated by each concentration in turn presented in descending order until an appropriate response is elicited; (3) the insects are random-sampled, *i.e.*, a different group is tested at each concentration and note taken of the percentage of each class which responds. Median values for the threshold may be developed from any of these procedures by the proper mathematical treatment (see Dethier and Chadwick, 1948). As will be shown below, use of these procedures on a comparative basis affords excellent opportunities for investigating the phenomenon of adaptation.

I. DEMONSTRATION OF ADAPTATION

Methods and results

Random Series. Several hundred one to three day old flies (*Phormia regina* Meigen) from a standard culture were mounted on sticks according to the method described by Dethier and Chadwick (1947). Just prior to testing, each fly was given water *ad libitum*. A series of sucrose solutions of doubling steps of concentration from 0.0005 *M* to 1 *M* was prepared. The flies were divided into as many groups of twenty each as there were concentrations of sucrose. Each group was tested at a different concentration. A test consisted of lowering the legs of each fly first into water until no proboscis extension was elicited and then placing the legs into the test solution for two seconds. The percentages of each group responding at each concentration were converted to probability units and plotted against the logarithms of the respective concentrations. The most probable value of the log concentration accepted by 50% of the flies was then determined according to the method of Bliss (1938).

Ascending Series. The same series of solutions as before was prepared. Each fly was tested as follows: (1) its legs were placed in water, and if a response was elicited, the animal was allowed to drink its fill; (2) when the response to water was negative, the fly was placed in 0.0005 *M* sucrose for two seconds; (3) if no response was forthcoming, the fly was transferred directly to the next higher concentration for two seconds and similarly on up the concentration series until a response was elicited. In no test was the proboscis ever allowed to touch the test solution. Once a fly had responded to a given concentration, it almost invariably responded to all higher concentrations. As soon as all flies had been tested the raw data were sampled in the following manner. A table with as many columns as there were concentrations was constructed. The specimens were now sampled, five at a time, in the order in which they had appeared for testing. For the first group of five the number accepting at the highest concentration was recorded in the table; for the next group, the number accepting at the next lower concentration; and so on in rotation until all of the flies used in the test had been recorded. The percentages accepting at each concentration were calculated from the totals in the columns and treated as above.

In an ascending series the responses of the population usually extended over ten doubling concentrations. Consequently, it was the custom to test a minimum of two hundred flies so that the *n* for each class was never less than twenty.

Descending Series. The method of running descending series differs from that of ascending series in the following respects. After being tested in water flies are presented first with a high concentration, *e.g.*, 1 *M*, known, as a result of informa-

tion derived from random series, to be above threshold. After two seconds each fly is then presented directly with the next lower concentration and so on down the series until the proboscis is withdrawn. When this occurs, the animal is retested against the starting concentration as a check against absolute refractoriness. If he continues down to the lowest concentration in the series with no sign of cessation of response, he is retested in water. Such a fly invariably drinks greedily, and the test is discarded. Not infrequently flies which are negative to water at the beginning of a run develop a desire for water in the course of the run. Data are accumulated and manipulated as already described. No significant difference in threshold is obtained if the feet are washed in water between successive concentrations provided the time consumed does not exceed a few seconds.

It is important to keep in mind the fact that descending series may be started at any supraliminal concentration.

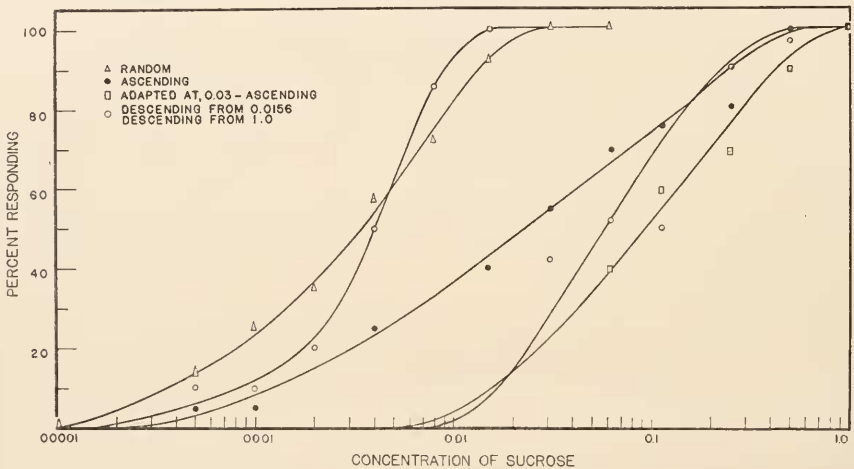


FIGURE 1. Change in the acceptance threshold of the blowfly to sucrose brought about by altering the order of presentation of different concentrations.

Adapted at One Concentration. It was feasible to start these series at any concentration, either subliminal or supraliminal. If, for example, a supraliminal concentration such as 0.03125 *M* was chosen as the starting point, each fly in turn was held with its feet in the solution until extension of the proboscis finally ceased. The animal was then run up the series in the usual manner until a fresh proboscis response was elicited. Again the data were random-sampled and treated as in the case of a normal ascending series. An alternative method was to random sample after adaptation. This procedure was carried out by dividing the flies into groups of twenty. Each fly in turn in group 1 was adapted, then tested at the next doubling concentration. The per cent responding was recorded. The members of group 2 were similarly adapted, then tested each in turn at the second highest doubling concentration and so on. If a subliminal concentration was chosen for adaptation, the feet were held in contact with the solution for ten seconds after which one of the procedures described above was followed.

Altogether, seven acceptance thresholds were determined by means of the techniques just described (see Section III): random sampled, ascending, descending from 1.0 *M*, descending from 0.0156 *M*, ascending after adaptation at 0.03125 *M*, random after adaptation at 0.0156 *M*, and random sampled after adaptation at 0.001 *M* (see Section III). Representative curves describing the distribution of these thresholds are seen in Figure 1. Statistical information relating to the median threshold values, standard errors, slopes and variance is given in Table I.

Discussion

It is clear from an inspection of Figure 1 that several different values for the acceptance threshold of sucrose by a given population of flies can be obtained and

TABLE I
Acceptance and rejection thresholds of Phormia regina as ascertained from different methods of presentation of stimuli

| Method of presentation | Median acceptance threshold | Log molar concentration accepted by 50% | $a \pm \text{S.E.}$ | $b \pm \text{S.E.}$ | \bar{x} | No. of flies tested |
|-----------------------------------|-----------------------------|---|---------------------|---------------------|-----------|---------------------|
| Random | 0.00356 | -2.449 ± 0.0332 | 4.983 ± 0.0531 | 1.596 ± 0.117 | -2.555 | 120 |
| Ascending | 0.023 | -1.632 ± 0.0966 | 4.972 ± 0.0992 | 1.028 ± 0.123 | -1.659 | 220 |
| Descending | | | | | | |
| From 0.0156 <i>M</i> | 0.00334 | -2.476 ± 0.0598 | 5.016 ± 0.136 | 2.285 ± 0.310 | -2.469 | 120 |
| From 1.0 <i>M</i> | 0.0474 | -1.324 ± 0.0739 | 5.450 ± 0.119 | 1.834 ± 0.268 | -1.079 | 240 |
| Adapted at 0.03125—then ascending | 0.0953 | -1.021 ± 0.0999 | 5.510 ± 0.146 | 1.810 ± 0.381 | -0.739 | 100 |
| Adapted at 0.001 random | | | | | | |
| 1 sec. | 0.0116 | -1.935 ± 0.0477 | 5.188 ± 0.104 | 2.242 ± 0.271 | -2.019 | 250 |
| 4 sec. | 0.0156 | -1.807 ± 0.0472 | 4.901 ± 0.176 | 3.753 ± 0.630 | -1.933 | 100 |
| 10 sec. | 0.0168 | -1.776 ± 0.0050 | 4.891 ± 0.0897 | 1.802 ± 0.234 | -1.782 | 250 |
| 30 sec. | 0.0114 | -1.942 ± 0.0439 | 5.041 ± 0.173 | 3.939 ± 0.613 | -1.932 | 80 |
| Adapted at 0.0156 random | | | | | | |
| 12 sec. | 0.0458 | -1.339 ± 0.0472 | 5.058 ± 0.158 | 3.356 ± 0.464 | -1.322 | 100 |
| 30 sec. | 0.0676 | -1.170 ± 0.0505 | 4.996 ± 0.146 | 2.895 ± 0.392 | -1.171 | 100 |
| Ethanediol in fructose | | | | | | |
| Random | 8.128 | 0.910 ± 0.018 | 5.281 ± 0.137 | 7.647 ± 1.059 | 0.946 | 120 |
| Ascending | 8.241 | 0.916 ± 0.024 | 5.220 ± 0.144 | 6.182 ± 0.900 | 0.951 | 160 |
| Fructose in ethanediol | | | | | | |
| Random | 0.142 | -0.849 ± 0.096 | 5.093 ± 0.122 | 1.276 ± 0.251 | -0.777 | 120 |
| Ascending | 0.142 | -0.848 ± 0.066 | 5.380 ± 0.150 | 2.364 ± 0.414 | -0.730 | 100 |

that the magnitude of these values depends upon the order in which stimuli are presented. It can also be shown (Section III) that time relations in the presentation of stimuli are of considerable importance. The data demonstrate that response to stimulation of the tarsi by sucrose is profoundly modified by previous stimulation. This effect of stimulation exhibits all of the characteristics of adaptation.

The curve describing the distribution of thresholds of a sample of flies which has been random-sampled can be taken as the baseline of sensitivity for this laboratory population at a given age and level of nutrition and water balance. To this baseline all other thresholds will be referred, because its median represents the lowest

concentration of sucrose which will elicit a response from 50% of the flies, a concentration which is effective if there has been no immediate previous stimulation. This basal value is 0.00356 M .

When successive concentrations of sucrose are presented in ascending order beginning at a concentration subliminal with respect to the random curve, the threshold is increased by a factor of approximately seven. In other words, individuals now fail to respond to solutions which are known to be capable of evoking a response if presented directly after water and in the absence of previous stimulation. Quite obviously the process of gradually increasing the stimulus by small increments from a subliminal value has caused a decrease of sensitivity to occur, so that a higher-than-normal concentration is finally required to trigger response. If this is so, it should be possible to effect a similar condition by prolonged exposure to a single selected concentration. This can be accomplished, as explained in the foregoing section, by placing the feet in a concentration which normally produces a response, waiting until the animal ceases responding, and then stimulating successively in an ascending series until the animal again responds. Similarly one can, after cessation of initial response, determine the final threshold randomly instead of successively. In any event the final threshold obtained depends upon the strength of the initial adapting solution. In the two cases tested the threshold is a concentration approximately three times that of the adapting concentration. Thus, it may be seen that the median value following adaptation at 0.0156 M is 0.04 M and following 0.03125 M it is 0.095 M . If adaptation is accomplished at a still higher concentration, the final threshold will be correspondingly higher.

Again, if the effects produced by previous stimulation partake of the nature of adaptation, one would logically expect that successive stimuli presented in decreasing order of concentration would yield a threshold value differing from those obtained with the foregoing methods. Further inspection of Figure 1 will show that this is indeed the case and that once again the value finally obtained depends upon the starting point of descent. When the initial stimulus is that which elicits approximately 100% response in the random series, *i.e.*, 0.0156 M , the final threshold does not differ greatly from the random series value. It is 0.00334 M . When the descent starts with 1 M , that which elicits 100% response from animals in an ascending series, the final threshold value (0.0474 M) is only slightly higher than the ascending value (0.023 M) but is many times higher than that of the other descending series. In other words, the final threshold value is determined by the point of departure.

These results naturally raise several critical questions. Can they be reconciled with the data of earlier workers? What are the respective contributions of the peripheral and the central nervous systems to the phenomenon? What is the nature of the process?

The failure of the majority of early workers to demonstrate clearly a difference in threshold with different techniques of presentation of stimuli, commonly ascending versus descending series, is due principally to the fact that such a long time interval was allowed to elapse between presentation of successive concentrations that recovery was essentially complete, and the effects of previous stimulation had been largely dissipated. Even under optimum conditions of presentation of stimuli the difference between ascending and descending threshold values is hardly demon-

strable if identical ranges of concentrations are employed in the test. Marshall (1935) and Eger (1937), working with honeybees and caterpillars, respectively, routinely allowed 15- to 20-minute intervals between stimuli; consequently, it is not surprising that no threshold differences were demonstrated. The differences that Weis (1930), Verlaine (1927) and Kunze (1933), working with *Pyrameis atalanta*, *Pieris rapae* and the honeybee, respectively, reported are not statistically significant. Again, failure to show pronounced differences may be laid to the selection of time intervals. Weis, for example, presented ascending series essentially as described in this study, but in her descending series interpolated a 15- to 20-minute rest period between successive stimuli. Moreover, as shown above, it is not to be expected that there would be a great difference between an ascending series and a descending one when the latter begins at the top concentration of the former. Minnich (1929), on the other hand, studying the responses of *Calliphora vomitoria*, was able to arrive at a clear-cut difference because he compared the threshold obtained from an ascending series run as in this study with a threshold obtained by an ascending series in which the intervals between stimuli were so long (15 minutes) that the series was tantamount to being random. A period of 15 minutes appeared ample for complete recovery.

Thus it may be concluded that the contradictions in the published reports are not real, that the data are actually in agreement, and that previous stimulation does indeed affect the sensitivity of the system at one or more points.

II. SITE OF ADAPTATION

Methods

In order to determine whether or not failure of response to threshold amounts of sucrose following previous stimulation results primarily from a change in sensitivity of the receptors themselves or to adaptation at some distance from the peripheral system, that is, at a site in the central nervous system, an attempt was made to devise a method for separating the two effects. This was accomplished in part by adapting one leg and then testing the sensitivity of the contralateral leg. Several techniques were tested before two were decided upon. The first consisted of mounting each fly with all legs fastened to the wax block except the prothoracic pair and then tying a piece of fine silk thread to one of the free legs. This leg could now be raised or lowered into the test solution at will. Each fly was run up an ascending series of solutions in the usual manner except that the fettered leg was held out of the solution. As soon as a threshold of response had been obtained with the free leg, the unexposed leg, together with the adapted leg, was placed in a solution which was less concentrated but which was known from random series to be above the threshold of sensitivity. Forty-three flies were tested by means of this exacting technique.

The second technique made use of a partitioned dish which contained 0.125 *M* sucrose in one compartment and water in the other. A fly with only the prothoracic legs free was made to straddle the partition. The labellum was removed to prevent drinking. A proboscis response followed as a consequence of stimulation of one leg by the sucrose. As soon as the fly had become completely adapted, *i.e.*, retracted the proboscis and ceased responding, the legs were thoroughly rinsed

in water, the fly was returned to the partitioned dish as before to insure that it was indeed adapted, it was again rinsed in water, and finally faced in the opposite direction and placed in the dish so that the adapted leg was now in the water compartment and the unexposed leg in the sucrose compartment. Thirty-six flies were tested.

Results and discussion

In every case in which hobbled flies were exposed successively to an ascending series of concentrations (first method), the fly afterwards failed to respond to a concentration below the ascending threshold when the unexposed contralateral leg was stimulated. A response could be elicited only by stimulating with a supra-liminal concentration. Clearly, then, in this experiment the animal had become refractory in that it failed to respond even when a peripherally unadapted leg was stimulated. This behavior suggests that adaptation is central, but the possibility remains that the unnaturalness of the fettered condition rather than chemical adaptation may have been the limiting factor. However, the results were identical regardless of whether the free or the fettered leg was adapted.

On the other hand, when the divided dish was employed for testing, 66.6% of the flies which had been adapted on one leg responded vigorously when the contralateral leg was stimulated. Three major interpretations present themselves: (1) sucrose has not been washed from the stimulated leg completely, as a result of which the test with the contralateral leg actually amounted to bilateral stimulation; (2) adaptation is indeed peripheral; (3) adaptation occurs at a center in the CNS where there is no pooling of the contributions from both sides of the body.

With regard to the first possibility it can only be said that experience from many other sources would argue in favor of the rinsing being complete. If rinsing has not been adequate, the fact that addition of stimulation from the other leg provokes a response is an indication that the adapted leg is still contributing to the CNS and at least is not fully adapted; hence, the initial cessation of response results from CNS adaptation. On the other hand, if rinsing has been thorough, the return of response when the contralateral leg is stimulated indicates either that the first leg has been completely adapted or that the center into which it leads has been adapted. In either case stimulation of the fresh leg would activate a different site in the CNS and the animal would respond. The possibility of solving this problem appears remote. It must be added that not one of the 33.3% which failed to respond would respond (after adaptation) when both legs were placed simultaneously in 0.125 *M* sucrose. A greater concentration did provoke a response. Clearly these cases are indicative of a change in the central nervous system.

While it is surely unlikely that there is no adaptation in the receptors themselves, the more acceptable conclusion, all facts considered, is that the process which is being measured represents predominantly a state which has been brought about at some level in the central nervous system. If this be so, the condition may be analogous to the non-sensory adaptation in the olfactory system of man (Adrian, 1950) or to the phenomenon of inattention in general. It is indeed unfortunate that the tarsal system has not yet proved vulnerable to attack by bioelectrical techniques.

III. TIME COURSE OF ADAPTATION

Methods

Three different experiments were designed as a means of supplying information necessary for the plotting of adaptation curves. The first two conform more or less closely to the classical method of securing data for adaptation curves. Flies were adapted for varying periods of time to a selected concentration and the threshold measured after each period of adaptation. The experiment was repeated for several adapting concentrations. In the first method the adapting concentration was above the threshold of response (supraliminal). The actual method of procedure involved placing each fly of a sample of twenty in the adapting solution until the proboscis was retracted. This event was taken to mark zero time. The fly remained in contact with the solution for one second after zero time, after which it was exposed to a higher concentration for two seconds and the presence or absence of a response noted. Each remaining fly of the sample was treated similarly. Now another sample of twenty flies was placed one at a time in the same adapting solution also for one second and then tested at higher solution number two; a third sample was tested at higher solution number three and so on until five different samples of flies had each been adapted at the same concentration for an identical period of time and then tested for response at five different high concentrations. The per cent responding at each concentration was then calculated and from these values was determined the acceptance threshold characteristic of flies which had been adapted at a given solution for one second. The entire procedure was repeated at the same adapting solution for a period of two seconds, three seconds, and so on until a sufficient number of data had been obtained to plot a curve for that particular adapting concentration. The experiment was repeated in its entirety for another adapting concentration.

Method number two differed from the foregoing in one respect only. The adapting solutions were subliminal. Since there was no proboscis response to these adapting solutions, zero time was taken as the time at which the tarsi first came into contact with the solution.

Method number three consisted simply of ascertaining the time required for complete adaptation at each of several different concentrations. Data were obtained for each concentration by placing the feet of a fly in the solution and recording the interval of time which elapsed between extension of the proboscis, which occurred almost immediately after the feet touched the solution, and retraction. One hundred flies were tested at each concentration. It should be emphasized that the mouthparts were at no time in contact with the solutions.

The results of these three experiments are summarized in Table I. Data obtained by method number three are plotted in Figure 2.

Discussion

The fact that the rise in threshold following adaptation to supraliminal concentrations (method one) is independent of the duration of stimulation, once the proboscis has been retracted, and is constant, suggests that the change in sensitivity has attained completion at the time of retraction. The magnitude of the completed change varies as the adapting concentration, as a comparison of thresholds after continued exposure to different adapting concentrations has shown (Section I),

but in each case it is complete. It follows from this that the development of adaptation must be studied at subliminal concentrations. When this is done (method 2) at 0.001 *M* for example, there are indications of an increase in threshold as the duration of continued stimulation increases. Thus, at zero time (no previous exposure) the threshold is 0.00356 *M*; at one second it is 0.0116 *M*, at 10 seconds

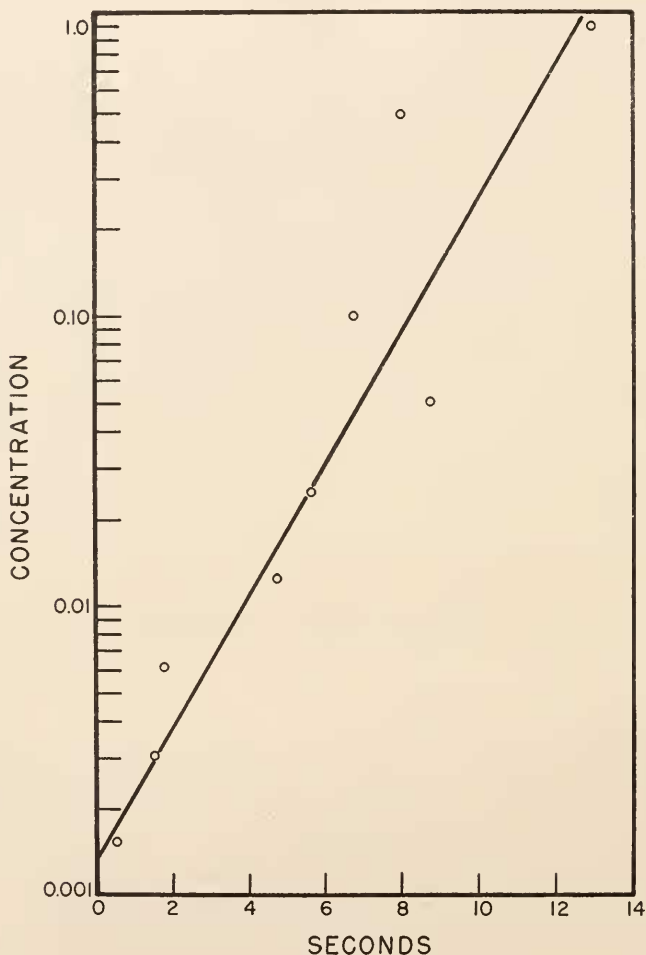


FIGURE 2. The relation between the concentration of sucrose employed as a stimulus and the time required for the cessation of response.

it is 0.0168 *M*. No further increase can be demonstrated up to and including 30 seconds. From these data it would appear that adaptation of the type being measured at 0.001 *M* is complete after one second. Increases from one to ten seconds, while progressing in the correct direction, are not statistically significant. Since it is manifestly impossible with the preparation at hand to investigate sensitivity changes occurring in fractions of a second, further indications as to the shape

of the curve of adaptation cannot be obtained. On the other hand, it is possible experimentally to ascertain the time necessary for complete adaptation at different concentrations (method 3).

As an examination of Figure 2 shows, the time for complete adaptation as measured by time to retraction of the proboscis increases as the logarithm of adapting concentration. The increase is from about 1.5 seconds at 0.003125 *M* to about 13 seconds at 1.0 *M*. These data are in agreement with those from methods one and two in that method one indicates adaptation to be complete when the proboscis is retracted and method two indicates that at 0.001 *M* adaptation is complete after one second or less. A less complete set of data obtained with fructose in ethylene glycol is in substantial agreement and shows an increase in adaptation time from about 4 seconds at 0.006 *M* to 7 seconds at 1.0 *M*.

Even though it has not been possible to construct adaptation curves for *Phormia*, the fact that a correlation with adapting concentration can be demonstrated permits one to compare certain aspects of the phenomenon in *Phormia* and man. Hahn (1933) and Hahn, Kuckulies and Bissar (1940) have measured the course of adaptation of a variety of substances at different concentrations. The forms of the curves differ considerably, but two facts are worthy of mention: adaptation is complete in anywhere from 10 to 30 seconds; the time required for total adaptation increases as the concentration is increased. The situation in *Phormia* is remarkably similar. Adaptation times vary from one to 13 seconds; the total time required increases as the concentration is increased. Over the range of lower concentrations, 0.003125 *M* to 0.05 *M*, the time required is proportional to the logarithm of molar concentration. From 0.05 *M* on there is no significant change in time with increasing concentration.

Continuous stimulation at constant intensity for long periods of time results in bursts of activity. For example, a fly with its feet exposed to 0.05 *M* sucrose will continue to extend its proboscis for a period of 13 seconds on the average. Thereupon, the proboscis is retracted. After a varying period of time extension recommences; then it again ceases. Such rhythmic activity has been observed over periods of continuous stimulation lasting as long as three hours. Thus far no correlation between frequency of activity cycles and concentration has been observed.

IV. SIMULTANEOUS STIMULATION BY MIXTURES OF SOLUTIONS

No experiments were designed specifically to demonstrate the presence or absence of adaptation to compounds other than sugars, but work done in another connection throws some light on this problem.

Thresholds measured by the random technique and in ascending series were compared for each of two different mixtures, fructose in glycol, and glycol in fructose. In other words, determinations were made of the acceptance threshold of fructose in glycol and of the rejection threshold of glycol in 0.05 *M* fructose. The pertinent data are summarized in Table I.

In the case of each mixture there is no difference in the threshold value obtained by the random and the ascending methods. The most logical explanation of this fact is that adaptation occurs to each component of the mixture and that the processes balance each other. Otherwise, were there to be adaptation to fructose alone, the acceptance threshold should be higher in the ascending series.

The acceptance threshold would be lower in the ascending series if there were adaptation to the glycol alone. Similarly, were there adaptation to fructose alone, the rejection threshold to glycol would be lower in the ascending series. Since adaptation to fructose in glycol most certainly does occur, as was shown in Section III, it must be concluded that in mixtures of the sort described either adaptation to the two components progresses apace or that cross adaptation occurs. This last is highly unlikely.

CONCLUSION

The universality of the phenomenon of adaptation, in nervous tissue especially, would have led one to infer that tarsal chemoreceptors in blowflies could hardly act otherwise. The chief problem heretofore had been to demonstrate the existence of the process. Once demonstrated the problem remained of separating the sensory and central components. Unfortunately, realization of this hope has been but partial. The present data indicate, as would also have been expected, that the process as measured by behavior represents a combination of both components. Indications are that the central process proceeds to completion more rapidly and that it is the one which is manifested in the majority of experiments.

A more ambitious hope lay in the expectation that knowledge of the time course characteristics of the process might lead to clues to the nature of the process of chemoreception. This has so far been a barren hope, not only in the field of insect physiology but in the study of the human sense of taste as well. More fruitful comparisons do exist. The times required for total adaptation in the two species are of the same order of magnitude although in man the process which is measured is almost certainly peripheral; the time to total adaptation increases as the adapting concentration increases.

The quickness of adaptation would tend to nullify the effectiveness of contact repellents; however, the corresponding speed of recovery counteracts this. Consequently, the existence of sensory adaptation to chemicals does not appear to be a factor which causes any appreciable reduction in the response of insects to repellents. It would thus appear that the process of adaptation plays no great part in the loss of repellency with time.

Certain characteristics of the response illustrate very beautifully some of the concepts of behavior recently reviewed by Lorenz (1950). In addition to exhibiting the type of adaptation described herein, it parallels in its action many other aspects of behavior seen in vertebrate animals. For example, under continuous stimulation of long duration the fly responds with bursts of activity; it shows an inertia of reaction in that removal of the stimulus, even when followed by rigorous cleansing in water, does not result in immediate cessation of response. On the other hand, proboscis extension *in vacuo*, that is, in the absence of stimulation after prolonged inactivity, has not been observed. The response is fully deserving of more intensive investigation because it offers unusual opportunities for establishing a neural basis for many commonly observed patterns of behavior.

SUMMARY

1. When receptors located in the tarsi of the blowfly *Phormia regina* are stimulated by solutions of sucrose, the insect responds by extending its proboscis.

2. The lowest concentration which would elicit a response from 50% of the population studied was taken as the acceptance threshold. The threshold value obtained depended upon the order in which different concentrations were offered for testing.

3. Adaptation was demonstrated by comparing threshold values obtained (1) by offering solutions in ascending series of concentrations, (2) in descending series, (3) by a random technique, (4) following exposure of the tarsi to subliminal concentrations in one case and supraliminal in the other. The process of adaptation which was measured represented predominantly a state which had been brought about at some level in the central nervous system.

4. The time required for adaptation increased as the logarithm of concentration. For sucrose it varied from one to 13 seconds. Stimulation by mixtures of glycol (unacceptable) and fructose (acceptable) resulted in adaptation to each component.

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